

Tidal influence on spatial dynamics of leopard sharks, *Triakis semifasciata*, in Tomales Bay, California

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Received 14 June 1999

Accepted 25 October 1999

Key words: movement behavior, tracking, elasmobranch, ultrasonic telemetry

Synopsis

We used ultrasonic telemetry to determine the movement directions and movement rates of leopard sharks, *Triakis semifasciata*, in Tomales Bay, California. To analyze tide and time of day effects, we surgically implanted transmitters in the peritoneal cavities of one male and five female leopard sharks, which we located during summer for three to five sampling sessions lasting 12 to 24 h each. All leopard sharks showed strong movement direction patterns with tide. During incoming tides, sharks moved significantly ($p < 0.0001$) towards the inner bay, apparently to exploit the extensive inner bay muddy littoral zones' food resources. On outgoing tides, sharks showed significant ($p < 0.0001$) movements towards the outer bay. During high tide, there was no discernible pattern to their movements ($p = 0.092$). Shark movement rates were significantly ($p < 0.0001$) greater during dark periods (mean \pm SE: 10.5 ± 1.0 m min⁻¹), compared with fully lighted ones (6.7 ± 0.5 m min⁻¹). Movement rates of longer sharks tended to be greater than those of shorter ones (range means \pm SE: 5.8 ± 0.6 m min⁻¹ for the 91 cm shark, to 12.8 ± 1.6 m min⁻¹ for the 119 cm shark), but the leopard sharks' overall mean movement rate (8.1 ± 0.5 m min⁻¹) was slower than other (more pelagic) sharks.

Introduction

Ultrasonic telemetry allows an observer to derive behavioral patterns by repeatedly establishing the two-dimensional position of an individual fish over an extended time period. Most telemetry studies have focused on pelagic fishes of open water systems showing that their movements can be related to the diel cycle (gray reef shark, *Carcharhinus amblyrhynchos*, McKibben & Nelson 1986; lemon shark, *Negaprion brevirostris*, Gruber et al. 1988; scalloped hammerhead, *Sphyrna lewini*, pups, Holland et al. 1992, Holland et al. 1993; and megamouth shark, *Megachasma pelagios*, Nelson et al. 1997), or depth and associated temperature gradients (blue shark, *Prionace glauca*, Carey & Scharold 1990; blue

marlin, *Makaira nigricans*, Block et al. 1992; striped marlin, *Tetrapturus audax*, Brill et al. 1993; short-fin mako, *Isurus oxyrinchus*, Holts & Bedford 1993; and juvenile lemon sharks, Morrissey & Gruber 1993). However, few tracking studies have focused on the more enclosed bays, yet these studies have recognized the influence of tidal stage on movement behavior (young dusky sharks, *Carcharhinus obscurus*, Huish & Benedict 1978; Atlantic stingray, *Dasyatis sabina*, Teaf 1978; young sandbar sharks, *Carcharhinus plumbeus*, Medved & Marshall 1983; age-0 summer flounder, *Paralichthys dentatus*, Szedlmayer & Able 1993).

The leopard shark, *Triakis semifasciata*, is native to inshore eastern Pacific waters of the mid-north latitudes, ranging from Mazatlan, Mexico to Oregon (Miller & Lea 1972). This shark is common in

California bays where they feed primarily on benthic prey in intertidal and subtidal areas (Russo 1975, Talent 1976, Webber & Cech 1998). Our objective was to determine the patterns of short-term movement directions and movement rates of leopard sharks in Tomales Bay, California, and the relationship of these movements to tide and time of day.

Materials and methods

Study site

Tomales Bay is located north of San Francisco Bay in Marin County, California. It is long (20 km), narrow (averages 1.4 km wide) and straight, having an average

depth of 3 m and a maximum channel depth of 20 m (Figure 1). Cumulatively, the total bay area is 24 km². Tomales Bay is characterized by an outer bay ranging from its mouth at the Pacific Ocean to 8 km inland and an inner bay ranging inland from 8 km to 20 km. The outer bay's bottom is largely a sand bar containing a deep channel along the west side of the bay, whereas the inner bay contains extensive intertidal and shallow subtidal 'mudflats' (Smith et al. 1991), hereafter referred to as muddy littoral zones (MLZ).

Fish collection

We collected six leopard sharks from Tomales Bay, California, on 16 June 1996, using short (30 min)

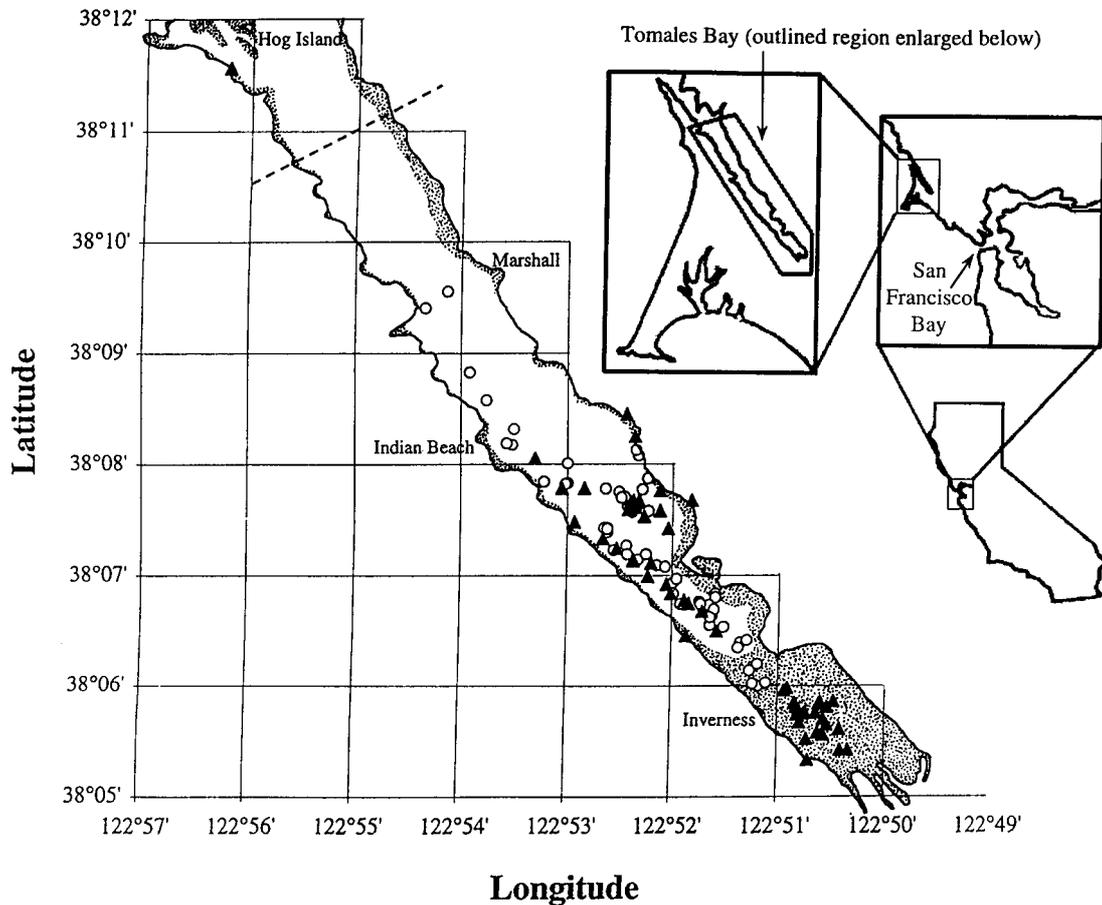


Figure 1. Leopard shark locations during high and low tide within Tomales Bay. During high tide (closed triangles), sharks were primarily located in the southern part of the inner bay or near inshore areas. During low tide (open circles), leopard sharks utilized the more intermediate and northern portions of the inner bay. The stippled area represents the MLZ and the dashed line separates the inner and outer bays.

gill-net (100 m × 3 m, 6 cm stretch mesh) sets (Haeseker & Cech 1993) placed in both the inner bay (near Indian Beach) and the outer bay (south of Hog Island, Figure 1). We placed captured sharks in sea water-filled coolers (12.6°C, 33.8‰ salinity) and immediately transported them by boat (10 min trip) and truck (40 min trip, in two 150 × 50 × 50 cm oxygenated seawater tanks) to the University of California, Davis, Bodega Marine Laboratory (BML), where we held them in an aerated, 2 kl round tank with continuous flows of seawater (9.7°C, 33.8‰ salinity).

Sonic transmitter implantation

We implanted individualized sonic transmitters in six sharks at BML. Each shark was anesthetized (MS-222, 0.2 g l⁻¹ sea water) until respiratory movements noticeably slowed, at which time we recorded total length and sex. We then placed the shark on a surgery table, and continuously circulated a more dilute MS-222 solution (0.05 g l⁻¹) over its gills during surgery. We inserted the ultrasonic transmitter (69 mm × 16 mm diameter, 21.4 g in air, Sonotronics, Tucson, Arizona) into the peritoneal cavity via a ventral, axial incision (2–3 cm long), 3 cm from the midline and 5 cm anterior to the pelvic fins. Transmitter weight to leopard shark body weight ratio (maximum: 0.4%) was well under the recommended 2% maximum (Winter 1983). We closed the incision with 5–6 silk sutures and swabbed it with erythromycin. Surgery lasted 12–20 min, and sharks were recovered at the BML in an aerated, 2 kl tank with continuous flows of seawater (9.7°C, 33.8‰) for 46 h (mean). We returned all leopard sharks to Tomales Bay in the oxygenated sea water tanks, released them on 18 June 1996 within 1 km of their capture site, and allowed 3 d for their re-orientation.

Ultrasonic telemetry

We periodically re-located one male (102 cm TL) and five female (91, 94, 94, 106, and 119 cm TL) leopard sharks for three weeks from 21 June through 12 July 1996. We located the five female sharks during each of the 12 to 24 h sampling sessions and the male during three of the five sessions. We chose sampling sessions by choosing days (21, 26 June, and 3, 8, 11 July) in which the high and low tides occurred at different times during the day-night cycle, which would allow tide and time of day to be analyzed as independent variables. Boat engine failures limited sampling to 12 h the

first day and 22 h the second day; all other sampling sessions were for 24 h continuous periods. Transmitters were typical pingers (Nelson 1987), operated at 75 kHz, repeating a number sequence that identified a specific individual at a 1 km maximum range (as specified by the manufacturer and confirmed in the field). A uni-directional hydrophone (Sonotronics DH-2) amplified and transmitted the transmitters' signals to the receiver (Sonotronics USR-5B, frequency range: 65–80 kHz) in the research boat. These signals allowed individual shark identification and directed the observers to its precise location. When the boat was positioned directly over the shark, the signal could be detected in a 360 degree arc (Winter 1983). We immediately recorded the time of day and position (latitude and longitude, Magellan 4000 global positioning system, accurate to 100 m). We measured water temperature and salinity using a salinity/conductivity/temperature meter (YSI 30) and depth using a sounding line. We then left the shark, undisturbed, and resumed locating other sharks. We attempted to relocate each shark every 45 min within our sampling session, allowing frequent calculations of movement directions and rates at various tidal stages and times of day.

Data analysis

To determine the movement directions between location data points, we converted the latitude (1 min = 1850 m) and longitude (1 min = 1475 m) differences between points into the straight-line distance (m). We plotted shark distances traveled, between consecutive data points, against true North and adjusted for Tomales Bay's geographical orientation (35° west of north). Sharks were considered to be moving in a direction (i.e., either towards the inner bay or towards the outer bay) if they moved twice as far in either of these directions as they did laterally (i.e., towards the eastern or western shores of the bay). Additionally, because of the global positioning system's 100 m error range, we included movement directions only for sharks moving > 200 m between consecutive location data points. We determined straight-line (minimum) movement rates by dividing the distance a shark moved between successive locations by the time interval it took the shark to travel between those locations.

For this study, we defined tidal stages by allotting 1 h on either side of high and low tide. We considered data points to be at high or low tides if they were within the 2 h peak of either tide. We considered sharks'

movement data to be in an incoming tide when they occurred between the 2 h low tide and the 2 h high tide that followed, and in an outgoing tide if they occurred between the 2 h high tide and the 2 h low tide that followed. If consecutive data points occurred during two tidal stages (e.g., the first data point occurred during a low tide and the second occurred during the following incoming tide), we used the median time between the data points to determine the tidal stage in which the shark spent most of its time. Movement rate and direction data were analyzed with ANOVA and Williams' goodness of fit (G statistic) tests, using the BIOM-pc statistical software. The Williams correction reduces the value of G, resulting in a more conservative test (Sokal & Rohlf 1995).

Results

Although we attempted to sample in a manner that would allow us to analyze tide and time of day effects as independent variables, boat engine failures prevented us from distributing our sampling effort equally over all combinations of tide and time of day. Specifically, we were unable to sample during a nighttime incoming tide on the first sampling day, which resulted in proportionally more incoming tide observations taken during the daytime. Therefore, in order to separate the effects of tide and time of day on shark movement direction we used goodness of fit tests to compare the frequency of observations for each tidal stage during the day and night (Table 1). We found that the proportion of observations for each tidal stage during the day differed significantly from those at night ($p \ll 0.0001$). Specifically, we got many more observations for incoming tides during the day than during the night and, conversely, many more observations for outgoing tides during the night than during the day. Therefore, inaccurate conclusions might be drawn regarding influences on shark movement direction if we analyzed time of day independent from tidal stage. To see if this was the case we then analyzed shark movement directions (i.e., toward the inner bay, toward the outer bay, and lateral) within each tidal stage in daytime versus nighttime observations. Using a significance level of $p = 0.0125$ (resulting in a total $\alpha = 0.05$ for the four tidal stages combined) we found no significant differences. That is, within each tidal stage, the proportion of sharks moving in each direction was approximately the same during the day and night (Table 1). We therefore concluded

that analyzing tidal stage independent of time of day was justified.

Another unavoidable source of error in telemetry studies is that it is impossible to control the number of observations on each individual. In this case, the goodness of fit tests showed that, for incoming, high, and low tides, there were no significant differences in the proportions of observations on each individual shark between day and night (Table 2). On the other hand, during outgoing tides, there were significant differences ($p = 0.001$). However, we feel that these sampling inconsistencies are ameliorated by the fact that the four sharks (i.e., 1, 4, 5, 6) for which we obtained the most samples have movements rates that are statistically indistinguishable from one another and the number of observations during the day and night are offsetting (Table 2). Therefore, we concluded that comparing rate of movement between day and night independent of individual sharks was justified.

Tidal stage significantly affected leopard sharks' movement direction in Tomales Bay. The proportion of sharks moving towards the inner bay (0.55) vs. outer bay (0.12) during incoming tide was significantly higher, and the proportion of sharks moving towards the outer bay (0.60) vs. inner bay (0.10) during the outgoing tide was significantly higher (both $p < 0.0001$, Williams' G statistic, Table 1). During high tide, there was no discernible pattern to their movements ($p = 0.092$). We were unable to distinguish differences among sharks ($p > 0.05$) except during low tide, when individual shark movement directions differed significantly from each other ($p = 0.015$). This precluded pooling data for all six sharks, and the low number of observations for each individual shark made it inappropriate to use the G statistic (Sokal & Rohlf 1995).

Tidal stage also influenced leopard sharks' location in the bay. During high tides the sharks were primarily located in the southern part of the inner bay and its shallower water over the extensive MLZ (Figure 1). During low tides sharks utilized the more intermediate and northern portions of the inner bay and its deeper water. Overall, leopard sharks inhabited water column depths from 0.3 to 8.4 m (mean = 2.4 m).

Leopard sharks' movement rates (range: < 1 – 37.4 m min^{-1}) were significantly influenced by time of day and, possibly, by body length. Movement rates were significantly higher during dark ($10.5 \pm 1.0 \text{ m min}^{-1}$) periods (peaking during the 24:00–3:59 interval), compared with lighted times of day

Table 1. Frequency of observations of shark movements (i.e., towards the inner bay, outer bay, or lateral) during each tidal stage during the day and night. Proportion MD refers to the overall movement directions of sharks within each tidal stage and time of day (i.e., day, night, or day & night). Proportion TS refers to the number of observations (for all movement directions combined) among each tidal stage during the day, night, or day & night. p-values (Williams' G statistic) compare the frequency of movement direction observations within each tidal stage between the day and night. The overall p-value ($\ll 0.0001$) compares the frequency of observations for each tidal stage between day and night.

Tidal stage	Shark movement direction	Time of day						
		Day		Night		p-value	Total (day & night)	
		Frequency	Proportion MD	Frequency	Proportion MD		Frequency	Proportion MD
Incoming	Inner bay	31	0.53	5	0.63	0.852	36	0.55
	Outer bay	7	0.12	1	0.13		8	0.12
	Lateral	20	0.34	2	0.25		22	0.33
	Total MD	58	1.00	8	1.00		66	1.00
	Proportion TS	0.45		0.09			0.30	
High	Inner bay	6	0.33	3	0.19	0.324	9	0.26
	Outer bay	4	0.22	3	0.19		7	0.21
	Lateral	8	0.44	10	0.63		18	0.53
	Total MD	18	1.00	16	1.00		34	1.00
	Proportion TS	0.14		0.18			0.15	
Outgoing	Inner bay	4	0.14	4	0.08	0.016	8	0.10
	Outer bay	12	0.43	34	0.69		46	0.60
	Lateral	12	0.43	11	0.22		23	0.30
	Total MD	28	1.00	49	1.00		77	1.00
	Proportion TS	0.22		0.54			0.35	
Low	Inner bay	8	0.31	5	0.29	0.845	13	0.30
	Outer bay	9	0.35	7	0.41		16	0.37
	Lateral	9	0.35	5	0.29		14	0.33
	Total MD	26	1.00	17	1.00		43	1.00
	Proportion TS	0.20		0.19			0.20	
	Total	130 (59% of total observations)		90 (41% of total observations)			220	

Overall day vs. night p-value $\ll 0.0001$.

($6.7 \pm 0.5 \text{ m min}^{-1}$, $p < 0.0001$, Figure 2). Although we were unable to meet the assumptions for statistical evaluation, longer sharks generally moved faster than shorter individuals (range means and maxima: 5.8 m min^{-1} and 21.4 m min^{-1} for the 91 cm shark, to 12.8 m min^{-1} and 37.4 m min^{-1} for the 119 cm shark; Figure 3).

Discussion

Special precautions were taken in this telemetry study so as to not influence the leopard sharks' natural behavior (Winter 1983). Rather than continually following them, we relocated sharks at intervals. This technique allowed for the least possible interaction with the sharks and reduced the chance of observer-induced disturbance. Additionally, those sharks located

in $< 1 \text{ m}$ water depth (typical of the inner bay's MLZ), were sampled via careful wading and pulling the boat with its hydrophone and receiver. Thus, possible disturbance from boat motor vibrations in shallow water was minimized.

Few elasmobranch telemetry studies have documented tidally-oriented movements, and of these, none were conducted for more than one 24 h continuous sampling period. Consequently, environmental factors such as tide and time of day could not be adequately analyzed as independent variables. Nevertheless, in temperate, estuarine habitats on the U.S. Atlantic coast, two (young) carcharhinids showed tidally oriented movements. The dusky shark and the sandbar shark moved predominately in the direction of the tidal current (Huish & Benedict 1978, Medved & Marshall 1983). Similarly, Teaf (1978) observed an extremely strong

Table 2. Frequency of observations of individual shark movement rates for each tidal stage during the day and night. Proportion IS refers to the individual sharks within each tidal stage and time of day (i.e., day, night, or day & night). Proportion TS refers to the number of observations (for all shark movement rates) among each tidal stage during the day, night, or day & night. p-values (Williams' G statistic) compare the frequency of individual shark movement rate observations within each tidal stage between the day and night.

Tidal stage	Individual shark	Time of day						
		Day		Night		p-value	Total (day & night)	
		Frequency	Proportion IS	Frequency	Proportion IS		Frequency	Proportion IS
Incoming	1	14	0.19	2	0.18	0.251	16	0.19
	2	16	0.21	1	0.09		17	0.20
	3	6	0.08	2	0.18		8	0.09
	4	14	0.19	4	0.36		18	0.21
	5	13	0.17	0	0.00		13	0.15
	6	12	0.16	2	0.18		14	0.16
	Total	75	1.00	11	1.00		86	1.00
Proportion TS	0.42		0.11		0.31			
High	1	4	0.16	3	0.16	0.777	7	0.16
	2	5	0.20	2	0.11		7	0.16
	3	3	0.12	2	0.11		5	0.11
	4	5	0.20	5	0.26		10	0.23
	5	5	0.20	3	0.16		8	0.18
	6	3	0.12	4	0.21		7	0.16
	Total	25	1.00	19	1.00		44	1.00
Proportion TS	0.14		0.18		0.16			
Outgoing	1	2	0.05	13	0.24	0.001	15	0.16
	2	7	0.18	6	0.11		13	0.14
	3	3	0.08	6	0.11		9	0.10
	4	11	0.28	7	0.13		18	0.19
	5	12	0.30	9	0.17		21	0.22
	6	5	0.13	13	0.24		18	0.19
	Total	40	1.00	54	1.00		94	1.00
Proportion TS	0.23		0.52		0.34			
Low	1	7	0.18	4	0.21	0.451	11	0.19
	2	6	0.16	6	0.32		12	0.21
	3	2	0.05	0	0.00		2	0.04
	4	8	0.21	3	0.16		11	0.19
	5	7	0.18	3	0.16		10	0.18
	6	8	0.21	3	0.16		11	0.19
	Total	38	1.00	19	1.00		57	1.00
Proportion TS	0.21		0.18		0.20			
Total	178 (63% of total observations)			103 (37% of total observations)		281		

relationship between direction of movement and the direction of the tidal flow in Atlantic stingray, using an attached float technique. Dubsky (1974) conducted the only previous tracking study of leopard sharks, in Morro Bay, California, and concluded that neither tidal current nor tide height was correlated with leopard shark activity (measured as distance travelled).

The majority of elasmobranchs' movement patterns have been predominately associated with the diel

cycle, emphasizing nighttime movements (reviewed by Nelson 1987). This pattern has been documented in many reef and inshore species: lemon shark (Gruber et al. 1988); gray reef shark (Nelson & Johnson 1980, McKibben & Nelson 1986); whitetip reef shark, *Triaenodon obsesus* (Nelson & Johnson 1980); scalloped hammerheads (Holland et al. 1992, 1993); Pacific angel shark, *Squatina californica* (Pittenger 1984); horn shark, *Heterodontus francisci* (Strong 1989); and

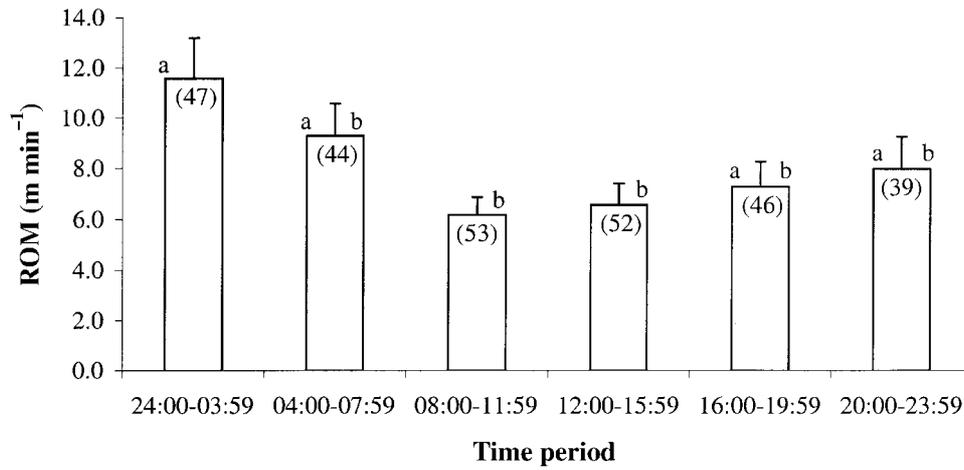


Figure 2. Diel influences on leopard shark rate of movement (ROM, m min^{-1} , mean \pm SE). Shark movement rates were significantly ($p < 0.0001$) higher during dark periods (peaking during the 24:00–3:59 h interval) than fully lighted ones. Different letters indicate statistically distinguishable differences among 4 h segments of the 24 h day; parentheses indicate number of measurements.

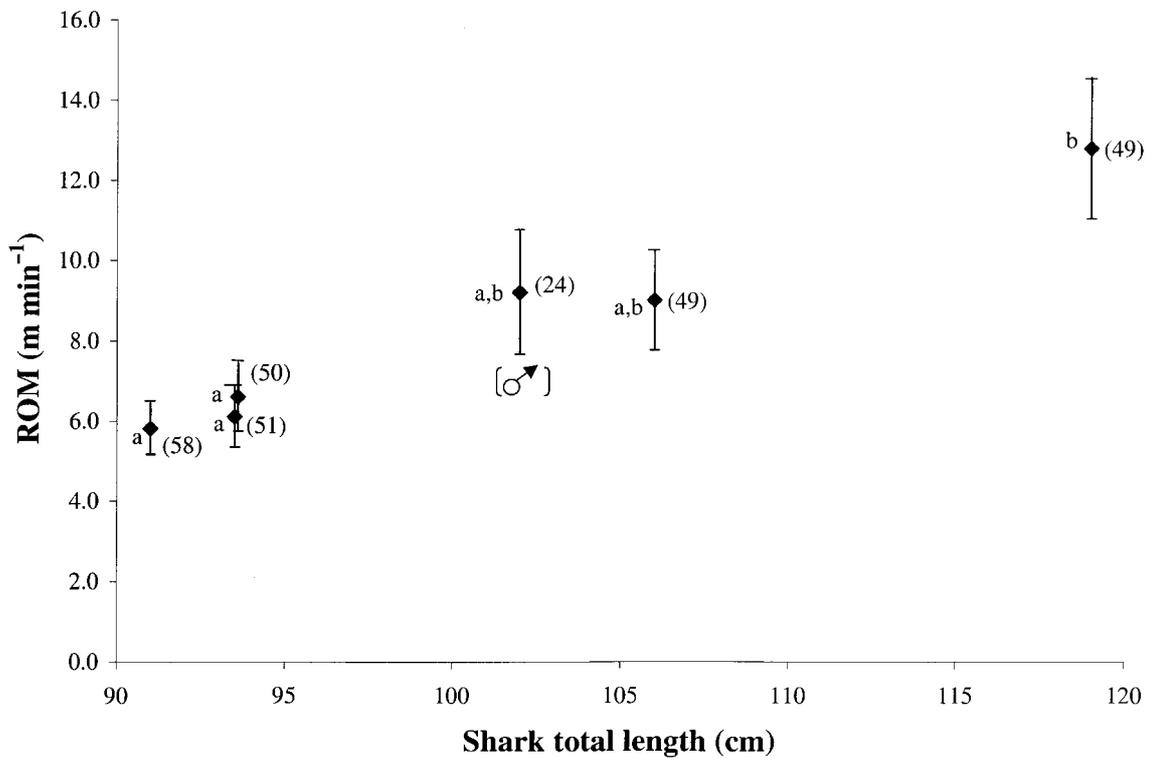


Figure 3. Rate of movement (ROM, m min^{-1} , mean \pm SE) and total length (cm) of individual leopard sharks. All sharks were female unless otherwise indicated. Different letters indicate statistically distinguishable groups; parentheses indicate number of measurements.

tiger shark, *Galeocerdo cuvier* (Tricas et al. 1981). The leopard shark movement rates we observed were significantly higher at night than during the day, and are consistent with this diel activity pattern.

However, shark movement directions are known to be affected by various factors. Lemon sharks oriented towards the sun, traveling east at sunrise and west at sunset (Gruber et al. 1988), while juvenile lemon sharks selected shallower and warmer areas within the mosaic of available habitats near Bimini (Morrissey & Gruber 1993). Scalloped hammerheads relate strongly to geomagnetic gradients around Gulf of California seamounts (Klimley 1993). Blue sharks are also thought to orient towards the Earth's magnetic field or oceans' electric fields, traveling in a steady direction through day and night (Carey & Scharold 1990). Blue sharks were also shown to migrate vertically as a means of behavioral thermoregulation (Carey & Scharold 1990), and, in a shuttle box experiment, smooth dogfish sharks, *Mustelus canis*, behaviorally thermoregulated by adjusting their ambient temperature, preferring a mid-day temperature peak and crepuscular minima (Casterlin & Reynolds 1979).

Relevant to the Tomales Bay ecosystem, bat rays *Myliobatis californica* moved according to a diel periodicity during summer (Matern et al. 1999). These rays moved towards the inner bay from 2:50 to 14:50 h which enabled them to feed within the MLZ while ambient temperatures were high, and they moved towards the outer bay from 14:50 to 2:50 h seeking the cooler, deeper water refuge after feeding. Hopkins & Cech (1994) hypothesized that bat rays in Tomales Bay behaviorally thermoregulate to minimize metabolic expenditures and increase assimilation efficiency. Because bat rays are metabolically very sensitive to temperatures in the 14 to 20°C range typical of Tomales Bay (Q_{10} : 6.81), they achieve significant savings in energy expenditure by being in cooler waters (Hopkins & Cech 1994).

In contrast to bat rays, our leopard sharks' movements corresponded most closely with tidal stages (Table 1). Leopard sharks significantly moved towards the inner bay with the incoming tidal currents, regardless of time of day, onto the MLZ presumably to exploit the food resources made available by the rising tides. While over the MLZ during high tides (Figure 1), there was no discernible pattern to their movements. This movement pattern is consistent with benthic foraging, and leopard sharks feed extensively upon benthic organisms (e.g., worms and clam siphons) that occur in

mudflat habitats. The echiuroid worm *Urechis caupo* makes up a significant portion of the leopard shark's diet in the inner bay (Webber & Cech 1998), and these sharks become highly reliant upon this food resource as they mature (Russo 1975, Talent 1976). Talent (1976) found *Urechis caupo* to be the most important food species in the diet of leopard sharks over 90 cm in length; the leopard sharks tracked in this telemetry study were all longer than 90 cm. Similarly, Atlantic stingrays move into marsh areas at high tide, presumably to improve their feeding potential (Teaf 1978).

Our visual observations also supported our telemetry data. During high tides we observed large numbers (> 30) of shoaling leopard sharks (averaging an estimated 120 cm TL) over the inner bay's MLZ in < 0.6 m of water. These large aggregations of leopard sharks appeared to be shoaling intraspecifically.

During outgoing tides, leopard sharks significantly moved towards the outer bay, regardless of time of day (Table 1), and at low tides the sharks were mostly located in the intermediate and northern portions of the inner bay (Figure 1). It appeared that during outgoing and low tides, the leopard sharks swam just far enough (mean: 1.2 km, sharks moving toward the outer bay during outgoing tides, $n = 46$) towards the outer bay, escaping extreme shallows and possible stranding, to a typical bay depth (ca. 3 m, Smith et al. 1991) without moving long distances. In fact, throughout the sampling sessions over the three-week study, the transmitter sharks mostly remained within the inner bay (Figure 1). This behavior should optimize their presumed high tide foraging activities in the MLZ and save swimming energy costs. Additionally, shorter movements, especially those in the same direction as tidal currents, can potentially save significant swimming energy. Scharold et al. (1989) measured leopard shark oxygen consumption rates at 14–18°C in a large swimming respirometer. Using their regression relationship for oxygen consumption rate and swimming velocity, our leopard sharks' overall mean movement rate of 8.1 m min^{-1} should increase total oxygen consumption by 6% in still water over Scharold's et al. (1989) estimated resting level. Although we did not measure tidal velocities in Tomales Bay, an estimated summer tidal velocity range in the southern half of Tomales Bay is 0.5 to 1 knot ($15\text{--}30 \text{ m min}^{-1}$, J.T. Hollibaugh personal communication). Because this range exceeds the leopard sharks' overall movement rate, tidally assisted swimming could cancel any increased swimming energetic costs, potentially conserving 6% of the leopard shark's

total energy expenditure while swimming with the tidal currents. Using oxygen consumption data to estimate total metabolic demands at these swimming velocities is probably valid, because even the fastest movement measured (37.4 m min^{-1}) is only 81% of the maximum sustainable velocity measured for leopard sharks of this size range (46.2 m min^{-1} , Graham et al. 1990). However, all of the fish movement rates are straight-line calculations and almost certainly underestimate the true movement rate if the shark made any deviations (e.g., lateral movements or bottom sitting) from the calculated path.

Although we were unable to meet the assumptions for statistical evaluation, longer leopard sharks tended to move faster (Figure 3) and range over longer distances than shorter ones. Convergent with Weihs' (1977) model, Parsons (1990) found that longer bonnethead sharks, *Sphyrna tiburo*, volitionally swam faster (cm s^{-1}) in an annular respirometer than smaller ones. In contrast, blacknose sharks, *Carcharhinus acronotus*, of various sizes (range = 45–87 cm TL, mean = 59) chose almost identical mean swimming velocities in a circular respirometer (range = 30.0 – 33.6 cm s^{-1} , mean = 31.6; Carlson et al. 1999). Our largest female leopard shark (119 cm TL) typically made long movements, once traveling from the MLZ in the inner bay all the way to Pelican Point by Hog Island in the outer bay, a distance of 14.22 km in 12 h and 5 min (a minimal, straight-line, movement rate of 19.6 m min^{-1}). The second largest female also showed long travels. The only male (102 cm TL) shark transmitted in this study also traveled widely at times. During the second, third and the first half of the fourth telemetry day, we were unable to locate the male leopard shark. Because of our extensive searches within Tomales Bay, we believed that the male shark had traveled to the mouth (not sampled) or out of the bay; returning on the fourth telemetry day traveling towards the inner bay.

Our results indicate that leopard sharks movement patterns are highly influenced by the tide, including movements into the MLZ at high tide presumably to forage (Russo 1975, Talent 1976, Webber & Cech 1998). Because leopard sharks are increasingly being sought for recreational and commercial harvest (Love 1996, Smith & Abramson 1990), they are susceptible to over-harvest due to their proximity to bays and along beaches, slow growth rates, long maturation times, low fecundities, and long gestation times (Kusher et al. 1992, Smith 1992). Fishing pressures can signifi-

cantly affect the leopard shark population and, because recruitment is largely based on parental stock size (Holden 1977), continued harvest without proper regulations may cause populations to decline. Many elasmobranchs are now being granted more protection from overharvesting (e.g., Compagno 1991, Leidy & Moyle 1998). If stricter harvesting regulations are required for leopard sharks, conservation strategies might benefit by focusing harvest regulations around their tidally influenced movements. Before this type of conservation strategy is employed, however, further research is needed to establish the pervasiveness of leopard sharks' tidally oriented movement pattern among seasons, sexes, and life intervals. For example, if gestating females have higher caloric needs and spend more time in the MLZ, fishing pressure could be restricted in these areas during the spring and summer months.

Acknowledgements

We thank P.B. Moyle for loan of equipment; L.E. Matern for surgical assistance; C.A. Myrick and C. Ackerman for technical assistance; the BML staff (especially J. Clegg, P. Siri, K. Brown, and C. Brigmann) for marine operations support; and P.B. Moyle, A.P. Klimley, and two anonymous reviewers for comments on the manuscript. Research was partially funded by U.C. Davis and by the U.C. Davis Agricultural Experiment Station (grant no. 3455-H to JJC).

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